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PLEOCOMA SPP. IN WESTERN OREGON CONIFEROUS FORESTS: OBSERVATIONS ON ADULT FLIGHT HABITS AND ON EGG AND LARVAL BIOLOGY[1] (COLEOPTERA: SCARABAEIDAE)

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In the early 1960's, I studied the feeding habits of *Pleocoma* larvae in some old-growth coniferous forests in western Oregon (Fellin, 1975). The study began shortly after Stein (1963) confirmed that *Pleocoma* larvae feed on the roots of forest trees. Five species of *Pleocoma* were studied—primarily *P. dubitabilis dubitabilis* Davis[2] (hereafter referred to merely as *P. dubitabilis*), *P. carinata* Linsley, *P. simi* Davis, and to a lesser extent *P. minor* Linsley, and *P. crinita* Linsley.

Incidental to that study, other studies were conducted and/or observations made on the biology, ecology, behavior, and distribution of Oregon *Pleocoma* spp. Many new localities were recorded and described. Based on these and other locality descriptions, the geographic distribution of all species of *Pleocoma* in Oregon was summarized and the habitats for *P. simi* and *P. carinata* were described (Fellin and Ritcher, 1967). Observations also were made on trapping male *Pleocoma* with female-baited traps (Fellin, 1968). Results of studies on the movement and distribution of *Pleocoma* larvae will be presented elsewhere.

Adult Flight

Since the earliest published record on the flight habits of *Pleocoma* males (Ricksecker 1887, 1888), entomologists have observed the flight habits of many species of *Pleocoma,* oftentimes incidental to collecting specimens for taxonomic study. Many observations have been made of environmental conditions or circumstances existing during male flight, especially with the species occurring in California.

These observations frequently have been interpreted as reflecting patterns of behavior of a particular species associated with a particular environmental condition, when, in fact, they may have been merely artifacts of collecting. For example, under certain circumstances, individual males or groups of males of some species may behave in a particular manner, while under another set of circumstances, they might behave altogether differ-

ently. One entomologist, who has observed and collected all known (and some "unknown") species and subspecies in California has concluded, in concert with two of his colleagues, that, ". . . thus far, the only real piece of information to emerge is that *Pleocoma* males will fly (or can fly but might *not*) at any time of day, during every conceivable climatic condition (appropriate to the season), and will exhibit nearly every form of behavior physically feasible in the process." (F. T. Hovore, personal communication.)

Concerning the Oregon species, Ellertson and Ritcher (1959) observed the flights of *P. crinita, P. minor,* and *P. oregonensis* Leach, and Ritcher and Beer (1956) published a few notes on the adult activity of *P. dubitabilis*. Nothing has been published until now concerning the flight of the two southwestern Oregon species, *P. simi* and *P. carinata*. The only known reference to *P. carinata* flight is a statement of Linsley's (1941) that three *P. carinata* "were captured in a rainstorm."

The observations presented in this paper on the flights and the factors associated with flights of some Oregon species, are not to be interpreted as an indication of a species-specific response to some environmental condition. Rather, they are presented merely to document the conditions that existed while I or others observed flights of *P. dubitabilis, P. simi* or *P. carinata*.

Flight Habits

Description of flight.—The most detailed observation of the flight of an Oregon species was made 11 October 1960 on the Umpqua National Forest, about 28 km northwest of Union Creek in Douglas County, at an elevation of approximately 850 m. W. I. Stein (personal communication) describes the flight of a series of *P. simi* as follows:

> "Beetles were flying in the timber at the same time as in the open. When flights were at a maximum, several beetles could be seen at once within sight in any direction. Flights were both low among the weeds and over head high, or a combination thereof. Some beetles circled, others flew in relatively straight flights either up or down hill. Beetles did not fly too fast, but it took a good trot to keep up with them when they made straight flights."

Many species of *Pleocoma* males differ greatly in their flight behavior (Davis, 1934a); this variability in flight behavior is often explained by whether males are "tracking" a pheromone or merely "dispersing," not yet having picked up the female scent (F. T. Hovore, personal communication).

Males of *P. hirsuta* have been observed to fly stronger, swifter, or more "purposefully" when (a) disturbed or frightened by collectors or predators

Table 1. Date, time of day and weather conditions for flights of *Pleocoma dubitabilis, P. simi,* and *P. carinata* in western Oregon coniferous forests in 1960 and 1961.[1]

Date	Time of day	Weather conditions[2]
	Pleocoma dubitabilis	
12 October 1960	0620–0655	Drizzling during period of flight, but hard rain earlier in morning
12 October 1960	1400–1600	—
21 October 1961	1300–1500	Overcast
22 October 1961	1400–1630	Light rain
29 October 1961	1300–1500	Clear sky, sunny
31 October 1960	1330	Occasional drizzles and windy
1 November 1961	1100–1215	Partly cloudy with intermittent sun
12 November 1960	1315–1445	—
19 November 1960	1330–1500	Raining
	Pleocoma carinata	
11 October 1960	1630–1745	Light drizzle (observer reported it was dark when some of flight was seen)
11 October 1960	1530	Drizzling rain
15 October 1960	1½ hours before daylight	Not raining
16 October 1960	1640–1700	Just beginning to rain
27 October 1961	0730	Overcast
2 November 1960	1400	Very light rain
12 November 1960	1200	Raining
20 November 1960	1500	Light rain just beginning
1 December 1960	—	—
16 December 1960	—	—
	Pleocoma simi	
11 October 1960	1400	Rainy and foggy
11 October 1960	1250–1600	Intermittent rain, overcast
11 October 1960	1200–1600	Raining lightly
14 October 1960	0300–0600	Clear, air temperature 5°C
14 October 1961	1700–1800	Not raining
23 October 1961	1015	Heavy shifting fog with rain
25 October 1961	1330	Overcast, occasional light mist
25 October 1961	0930	Overcast, air calm and mild, occasional drops of rain

Table 1. Continued.

Date	Time of day	Weather conditions[2]
28 October 1960	1100–1200	Foggy with light rain
October 1960	after 1500	Light rain
2 November 1960	1300	Overcast, fog and very light rain
2 November 1960	1115–1145	Overcast with light rain
16 November 1960	1355–1430	Overcast, light fog, heavy drizzle, 2 inches of snow on ground yesterday, ground bare today
17 November 1960	0820–1400	Overcast, raining
13 December 1961	afternoon	Fairly heavy rain

[1] All flights of *Pleocoma dubitabilis* were observed by the author in a Douglas-fir stand at McDonald Forest, 8 km north of Corvallis, Oregon, Benton County. Flights of *Pleocoma simi* and *Pleocoma carinata* were seen by various people in mixed coniferous forests primarily on the Umpqua and Rogue River National Forests in Douglas, Jackson, and Josephine Counties in southwestern Oregon.

[2] The subjectivity of such terms as "drizzle, light rain, drizzling, rain" etc., is recognized. Although each can mean different intensities of precipitation to different people, the terms are presented in the words of the individuals making the observations.

and (b) near the end of a given activity period (F. T. Hovore, personal communication).

Time of day of flight.—Males of *P. dubitabilis, P. simi,* and *P. carinata* were observed flying from predawn until late afternoon and early evening (Table 1). The earliest flights observed were those of *P. simi* at 0300 14 October 1960 and *P. carinata,* 1½ hours before daylight 15 October 1960. The latest flights were about 1745–1800 11 October 1960 and 14 October 1961 for *P. carinata* and *P. simi,* respectively. Though the data in Table 1 indicate periods during the day when beetles were observed flying, they do not preclude the possibilities of flights occurring from late evening until early morning when observers were not likely to be in the forest.

An unconfirmed, but reliable, report of an adult male *Pleocoma* (*carinata*?) captured in flight at 2330 is substantiated by reports that males of other species of *Pleocoma* fly at night. In November 1949, males of *P. conjungens* were taken almost continually from 2200 to 0600 hrs. during a steady light rain and a nearly full moon (Hazeltine, 1950). *Pleocoma fimbriata* males are reported to fly at dusk (Hopping, 1920), and *P. marquai* males will fly throughout the night while rain or snow is falling and at dusk for several days thereafter (Hovore, 1972). F. T. Hovore (personal communication) also reports that an increase in rain intensity initiated small flights of *P. conjungens lucia* and *P. blaisdelli* at 2330 and 0200 hrs., respectively.

Time of year of flight.—In 1960 and 1961, males of all three species, *P. dubitabilis, P. carinata,* and *P. simi,* flew for the first time on 11–12 October. The last *P. dubitabilis* flight was observed on 19 November 1960 and most major flights of *P. simi* and *P. carinata* were last observed between 17–20 November. However, some *P. carinata* males were still flying as late as 1 and 16 December 1960 and a *P. simi* flight was reported by Bureau of Land Management foresters near Myrtle Creek in Douglas County on 13 December 1961.

As far as *P. dubitabilis* is concerned, observations presented in Table 1 generally support earlier ones. In 1954, Ritcher and Beer (1956) report *P. dubitabilis* began flying on 16 October (at Forest Grove) and continued, when conditions were favorable, through the second week in November. In 1955, males first flew on 3 October (at McMinnville). That year, at the McDonald Forest study area, flight began shortly before 8 October and continued until 4 November (Ritcher and Beer, 1956).

The peak of male activity for *P. oregonensis* occurs in October and November (Ellertson, 1956).

Other species of *Pleocoma* are known to fly late into the winter. *Pleocoma crinita* is reported to have sporadic flights as late as March (Ellertson and Ritcher, 1959). *Pleocoma hoppingi* males have been collected in flight as late as 5 February (Linsley, 1941) and 16 March (F. T. Hovore, personal communication) in Yosemite National Park in California. Flight of *P. marquai* males usually begins in early October and can continue until early December in years of relatively low rainfall (Hovore, 1972). Two males of this species were taken in flight on 6 January 1979 (F. T. Hovore, personal communication). Specimens of *P. rubiginosa* Hovore have been collected in blacklight traps from January to April, and *P. reflexa* males are known to fly from late November to mid-January (Hovore, 1972).

I have an additional unconfirmed report of *Pleocoma* males flying as early as late August. On 8 November 1961, I received a letter from Gordon Walker (personal communication) describing several collections he had made of *Pleocoma* males that fall. The letter read, in part, as follows:

> "Also around the week of the 24th of August, I caught one about 11:30 one night while on a fire in the Neil Creek area. The exact location is T40S, R1E, SE¼NE¼ section 12. I didn't have any place to put the thing so I took the head off a flashlight and put it in behind the reflector. It would have worked fine, but I put the flashlight with several others and couldn't locate it after that."

Although I did not see the specimen for positive identification (which could make this record somewhat suspect), I consider this a reliable report since Walker had forwarded specimens from several collections to me in the fall of 1960 and 1961. He reportedly caught the beetle 9 km south-southeast of

Ashland (Jackson County) and a similar distance from the California border, at a site between the known distributions for *P. carinata* and *P. simi*. It could have been either one of these species or *P. shastensis* or one of the other northern California species.

The time of year of flight may also be influenced by certain weather conditions, particularly fall rains. Hovore (personal communication) indicates that in the mid-1970's when fall rains were late, he observed species (*P. australis, P. marquai,* and *P. tularensis*), which normally fly from late September to early November, flying from January to March. The following year was characterized by unusually early heavy rains, and he took the same species in flight in mid-September. He concludes that ". . . under 'normal' circumstances, one can safely 'predict' the approximate flight seasons of various species according to their usual levels of responsiveness to precipitation . . . ," but in years of very early, very late, or particularly cold seasons, flight times can often be off as much as 2 or 3 months.

Environmental Factors Associated with Flights

Moisture.—Probably the greatest single factor affecting flight of adult male *Pleocoma* is rainfall. As noted by Ellertson and Ritcher (1959), "The autumn and winter seasons with their rain and saturated atmosphere have long been associated with flight of *Pleocoma* males." However, as Hovore observed (personal communication), "The actual presence of falling rain though 'preferred' by certain species (such as *puncticollis, australis, marquai*) is not entirely necessary."

The first flights of the year seem to follow general fall rains and subsequent flights are often, but not always, associated with day to day precipitation. At a study site at McDonald Forest, 8 km north of Corvallis (Benton County) the first *P. dubitabilis* flights were observed in 1960 on 12 October; two flights were observed, one between 0600–0700 and another between 1400–1600 hrs. Although 4 cm of rain had fallen at that site between 1 September and 12 October, these and subsequent flights probably were triggered by the 3.60 cm of rain that fell between 6 and 12 October, as shown below:

Date	cm
1 September–5 October	0.40
6–8 October	2.55
9 October	0.15
10–11 October	0.00
12 October	0.90

Ellertson and Ritcher (1959) note that at least 2.5 cm of rain falls between 1 September and first flights of *P. crinita* males at Hood River.

Adult males of *P. simi* and *P. carinata* flew for the first time in 1960 on

11 October when flights at five localities were documented by as many observers on the Umpqua and Rogue River National Forests in Jackson and Douglas Counties. The distance between the two furthermost observed flights was about 112 km.

These five flights occurred after the third general rain in western Oregon. A general rain fell in western Oregon between 1–4 September (U.S. Weather Bureau, 1960a). The next general rain fell 6 October and lasted for 3 days (U.S. Weather Bureau, 1960b). On 9 October, rain was scattered and, on 10 October, no rain or a trace was reported. On 11–12 October, a general rain fell again. Two factors were common to all five flights: (1) each flight was observed at some period between 1200 hrs. and dark and (2) rain was falling at the time each flight was observed.

Observations by four individuals who observed and collected *P. simi* in flight show how closely—after the first general fall flights—male flights appear to be related to precipitation. (1) A collector at a site 29 km northwest of Union Creek (Douglas County) reported that rain began falling at 1300 2 November 1960 and beetles became abundant locally; none had been seen earlier in the day. (2) In October, another collector (D. J. Tandy, personal communication) reported that, at a site 26 km west-northwest of Diamond Lake (Douglas County), when a sprinkling rain began falling at 1500, beetles came out and many were in flight almost immediately. (3) On 11 October 1960 a third collector (Jerry Conner, personal communication) working on the Rogue River National Forest 11 km north of Prospect (Jackson County) reported that a few beetles were seen shortly after noon and that the number increased the longer it rained. (4) The fourth flight was described (W. I. Stein, personal communication) as follows:

> "Arrived at Falls Unit (27 km northwest of Union Creek, Douglas County) shortly before 12 o'clock (noon, 11 October) weather first was calm, chilly and overcast with brief interludes of diluted sunshine. Then breeze came up which made it colder and more uncomfortable. Shortly after 12:30 p.m. overcast became complete rapidly. Some wind developed, and a few drops of rain started falling. Simultaneously beetle (*P. simi*) activity became evident. The first one was sighted and captured at 12:50 p.m. Captures averaged nearly one a minute for the next half hour, then flights waned as did the rain. Within another half hour rain began again but beetle flights did not increase. Occasional beetle flights were seen until about 4:00 p.m. when heavy rain began."

The fall flights of these three Oregon species following the onset of fall precipitation are similar to those reported for many California species. Adult males of *P. linsleyi,* at least at the type locality, appear to begin flight only after the area has received over 7.5 cm of rain (Hovore, 1971). Hazeltine

(1952) reported that *P. puncticollis* males usually fly during the second or third general rain and that *P. fimbriata* males begin flying after the first few soaking rains (Hopping, 1920). Recently, Page and Fisher (1976) caught four males of *P. hirticollis vandykei* one day after the second rain of the season south of San Jose, California. According to Hovore (1972), adult activity of *P. marquai* in the vicinity of the type locality begins during or shortly after the first precipitation of the fall season, usually in early October. Males of *P. reflexa* have been collected only after an area has received several cm of precipitation (Hovore, 1972).

Although the above reports document the close association of beetle flights with rain, males of some Oregon species have been observed to fly in clear weather. On 29 October 1960, I observed about ½ dozen *P. dubitabilis* males flying between 1300–1500. It was a perfectly clear, cloudless day with air temperature 12°C. In the preceding 2 days, however, more than 2 cm of rain had fallen at that study site. On another clear day, 11 November 1960, no beetles were observed flying although rain had fallen all day on the 10th. On 14 October 1960, another collector observed *P. simi* males flying between 0300–0600 in clear weather in a forested area 8 km south of Eugene in Lane County.

Similarly, many of the California species are also known to fly in clear weather. A male *P. sonomae* was observed flying at sunset in clear cool weather in Marin County, California (Hazeltine, 1952). Smith and Potts (1945) reported *P. hirticollis vandykei* flying in late afternoon sunshine. Rivers (1889) mentions that it is the habit of *Pleocoma* to travel both by day and night, in sunshine or rain. Hovore (1971) reports that *P. nitida* Linsley does not require immediate precipitation for flight activity. He collected specimens, ". . . approximately 4 hours after rain had ceased and under clearing sky conditions." Hovore (1972) also reports that *P. marquai* will fly at dusk (for several days after a rain or snow) during weather conditions varying from heavy overcast to bright afternoon sunlight. He also collected a male *P. reflexa* shortly after dusk following a day of clear cold weather.

Male adult *Pleocoma* are also reported to be attracted to pools of water (Davis, 1934a), small streams and water-filled ditches or puddles (Ellertson, 1958; Linsley, 1957). Light reflected from the surface of the water apparently attracts the beetles. On 14 October 1961, Frank Wilson (personal communication) wrote that he "creamed" 37 *P. simi* males from the surface of puddles of water in the center of a clearcut on the Umpqua Forest east of Idleyld Park. Hovore (personal communication) has taken males of at least seven species from the surface of puddles, pools, and forebays in California.

Temperature.—I observed flights of *P. dubitabilis* when temperatures were as low as 6°C and as high as 15°C. On 5 November 1954, Ritcher and

Fig. 1. *Pleocoma* female with some of her eggs showing how they were laid in spiral fashion as she moved upward through the soil. (The eggs fell from their niches when collected and had to be replaced for the photograph.) (actual size)

Beer (1956) observed *P. dubitabilis* males flying when air temperatures were 10.5°C. One *P. simi* flight was observed in clear weather when the air temperature was 5°C.

On at least three occasions, adult males of Oregon species have been collected in areas where forest residue (slash) was being burned or where natural forest fires were being controlled. On 14 October 1961, *P. simi* males were flying in a clearcut area, 35 km east of Idleyld Park, Douglas County, where burning forest residue was accompanied by considerable smoke. It was not raining at the time. Later, on 23 October, *P. simi* males were flying

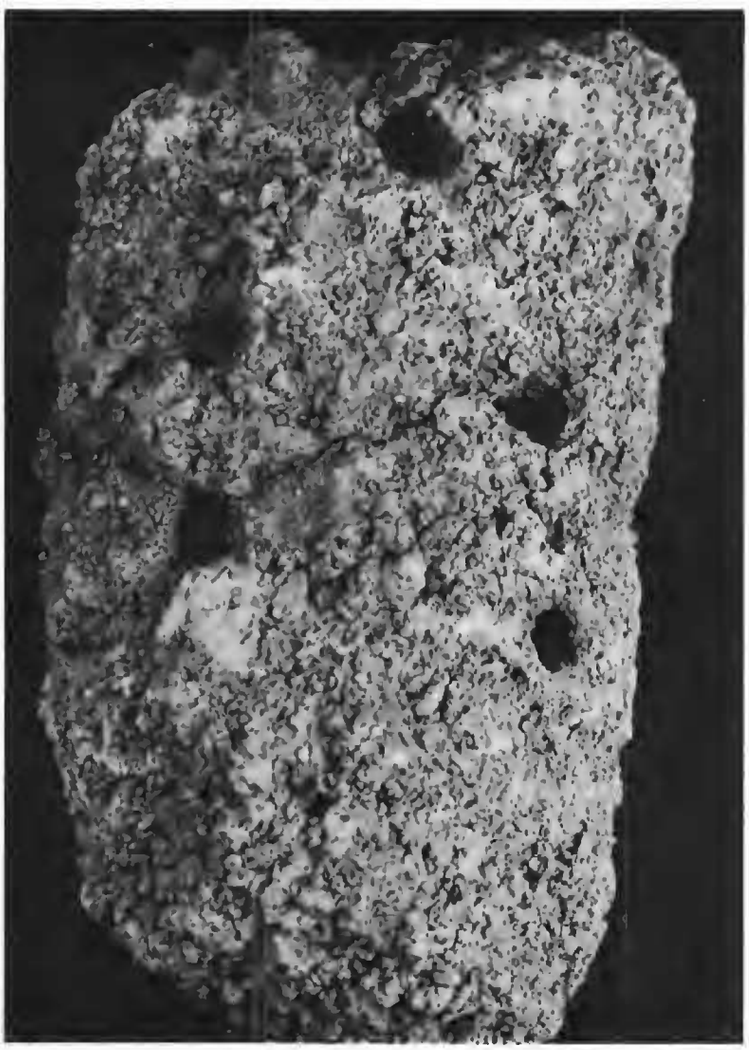

Fig. 2. Portion of vertical core of packed and pulverized soil. Burrows in the soil were made by second stage *Pleocoma dubitabilis* larvae moving outward from egg niches. Larvae were still in the burrows when the core was collected on 12 November 1960 (2×).

in another clearcut area, 14 km northeast of Tiller, Doulgas County, where slash had recently been burned. During this flight there was heavy shifting fog with rain. I have already mentioned the adult male reportedly caught by an individual fighting a forest fire on 24 August 1961. Whether increased air or soil temperatures during these fires had any relationship to the respective beetle flights is not known. It is possible that heat produced by the fires could have stimulated adult male beetles to emerge and fly, particularly if flights have already occurred and/or if males were in the litter close to the soil surface.

Egg and Larval Biology

With the exception of the studies of Ellertson (Ellertson and Ritcher, 1959) of *P. crinita, P. minor,* and *P. oregonensis* in Hood River and Wasco County orchards, little ecological information exists or has been published

concerning the soil-inhabiting stages, particularly for *P. simi, P. carinata,* or *P. dubitabilis* in the coniferous forest environment. My observations, though fragmentary, on the egg and larval biology for these three species are presented here.

In the laboratory, all eggs and larvae collected in the field and larvae developing from eggs laid in the laboratory were reared in small salve tins lightly packed with sifted soil. The tins were kept in a temperature cabinet equipped with a fan and heating unit to maintain constant temperature. Cabinet temperature was periodically adjusted to conform to soil temperature 75 cm deep at a study site at McDonald Forest, 8 km north of Corvallis.

Egg Biology

Eggs of *P. simi* and *P. carinata* are dull white in color and ellipsoidal in shape similar to eggs of *P. dubitabilis* (Ritcher and Beer, 1956), but they do not have the yellowish tinge characteristic of eggs of *P. crinita, P. minor,* and *P. oregonensis* (Ellertson, 1958).

Manner of deposition.—Other biologists have described how *Pleocoma* females deposit their eggs. Eggs are deposited individually beginning at the bottom of a burrow and moving upward in a spiral fashion within a vertical core of pulverized soil (Ritcher and Beer, 1956; Ellertson, 1958; Ellertson and Ritcher, 1959). The process has never been illustrated, however. Figure 1 shows an expired female with a portion of the clutch of eggs she has laid. The core of soil within which eggs are laid is often so tightly packed that it can be removed from the ground intact (Fig. 2).

Size of eggs.—All field-collected and laboratory-reared eggs were measured to the nearest 0.15 mm with a stereo microscope, one ocular of which was equipped with a calibrated micrometer. Laboratory-reared eggs of both *P. simi* and *P. carinata* are larger than those of *P. dubitabilis,* and 1-week-old *P. simi* eggs seem to be a bit longer than those of *P. carinata,* but about the same width (Table 2).

As with other insects (Counce, 1961), *Pleocoma* eggs enlarge during development. Eight-week-old eggs of both *P. carinata* and *P. dubitabilis* were both longer and wider than they were when they were 1 week old.

It appears that laboratory-deposited eggs are generally smaller than those laid under natural conditions in the field. This is due, no doubt, to the artificial conditions of the laboratory and the periodic handling of the females. Ninety field-collected *P. dubitabilis* eggs of unknown age averaged 5.33 and 4.31 mm in length and width, respectively. These field-collected eggs are larger than 8-week-old eggs laid in the laboratory (Table 2).

Number of eggs laid.—The total number of eggs deposited by single *P. dubitabilis* females in the field and in the laboratory was as follows:

Field	Laboratory
64	41
63	39
41	21

Table 2. Size of laboratory-reared *Pleocoma* eggs shortly after oviposition (1 week) and just before producing larvae (8 weeks).

Species	One week old			Eight weeks old		
	Number of eggs	Average (mm)		Number of eggs	Average (mm)	
		Length	Width		Length	Width
Pleocoma dubitabilis	96	4.53	3.00	84	4.99	3.89
Pleocoma carinata	67	4.95	3.24	56	5.36	4.18
Pleocoma simi	83	5.06	3.24	—	—	—

In the laboratory, two *P. carinata* females laid 34 and 33 eggs, respectively, and two *P. simi* females deposited 45 and 42 eggs, respectively. Two *P. oregonensis* females deposited 35 and 48 eggs, respectively, in the laboratory (Ellertson, 1956); however, Ellertson (1958) found considerable variation in the number of eggs deposited by *P. crinita, P. minor,* and *P. oregonensis*. Ritcher and Beer (1956) found that the total egg capacity of five *P. dubitabilis* females was 61, 59, 53, 51, and 33 eggs, respectively.

Depth of oviposition.—Six egg clutches of *P. dubitabilis* females exhumed from the soil indicate the depth at which oviposition took place as follows:

Date observed	Depth of eggs or small larvae[3]	
	Uppermost (cm)	Lowermost (cm)
7 May 1960	17.5	unknown
8 July 1960	47.5	58.0
15 August 1961	20.0	30.0
12 November 1960	17.5	unknown
12 November 1960	17.5	45.0
12 November 1960	31.0	45.0

Three more females collected on 31 March and 13 and 14 April at depths of 25, 34.5, and 17.5 cm, respectively, later oviposited in jars in the laboratory. Whether oviposition would have occurred at the depths at which the females were collected is unknown. On 23 July 1954, Ritcher and Beer (1956) found a single *P. dubitabilis* female that had deposited 50 eggs at a depth between 30 and 49 cm in the soil.

Table 3. Date and depth that dead adult *Pleocoma* females were collected in the soil in 1960 and 1961.

Species	Date	Depth (cm)
Pleocoma dubitabilis	22 April 1960	40
	7 May 1960	40
	7 May 1960	42.5
	8 July 1960	45
	25 August 1960	37.5
	25 August 1960	27.5
	12 November 1960	27.5
Pleocoma dubitabilis	31 March 1961	27.5
	29 April 1961	35
	29 May 1961	40
	28 June 1961	25
	6 August 1961	32
	21 August 1961	25
	13 September 1961	22.5
	21 October 1961	37.5
	22 December 1961	35
Pleocoma simi	16 June 1960	35
	8 October 1960	17.5
	14 October 1960	25
	7 January 1961	27.5
	7 January 1961	25
	7 December 1961	55
Pleocoma carinata	3 January 1961	52.5
	3 January 1961	52.5
	10 May 1961	15

Dead *P. dubitabilis*, *P. simi*, and *P. carinata* females were often collected in the soil. These females could have failed to emerge from the pupal cell and died there, or could have emerged from the pupal cell but died before reaching the soil surface. More likely, however, these females died after having spent themselves in oviposition, so the depth at which they were collected probably represents the depth of the uppermost egg laid. The date and depths at which these dead females were collected are shown in Table 3.

Time and rate of oviposition.—Two *P. carinata* females collected in the field on 3 January 1961 and two *P. simi* females collected on 26 May 1961 were removed to the laboratory, placed on packed, sifted soil in Mason jars, and examined periodically after 30 April. They began laying eggs soon after 30 May and continued until about 21 June. Between 14 and 21 June, the two *P. simi* females laid 4.6 and 4.7 eggs per day, respectively, and the two *P. carinata* females laid 3.3 and 4.7 eggs per day, respectively.

Table 4. Earliest and latest dates at which larvae hatch from eggs, for the Oregon species of *Pleocoma*.[1]

Species	Dates of larval hatch		Number of eggs observed
	Earliest	Latest	
Pleocoma dubitabilis	21 August	21 September	145
Pleocoma simi	8 September	15 September	6
Pleocoma carinata	3 September	8 September	43
Pleocoma crinita	21 July	12 September	24
Pleocoma minor	15 July	21 August	16
Pleocoma oregonensis	25 July	27 August	—

[1] Data for *P. crinita, P. minor,* and *P. oregonensis* from Ellertson (1956) and Ellertson and Ritcher (1959).

Three *P. dubitabilis* females began ovipositing in the laboratory just prior to 9 June 1961 and the last eggs were laid between 26 June and 2 July. From 10 to 25 June, these *P. dubitabilis* females laid an average of 1.3 eggs per day per female, considerably less than the number observed for *P. carinata* and *P. simi*. In 1955, Ritcher and Beer (1956) observed *P. dubitabilis* females laying eggs in late May and still in the process on 18 June.

Most adult females die shortly after depositing their last egg. Six females (two each of *P. dubitabilis, P. simi,* and *P. carinata*) deposited their last eggs between 21 June and 2 July in 1961 and died between 2 and 9 days later; however, a third *P. dubitabilis* female lived for 45 days after laying her last egg.

Duration of egg stage.—Laboratory-reared *P. dubitabilis, P. simi,* and *P. carinata* remained in the egg stage for 91, 89, and 81 days, respectively. This compares to 69 and 62 days in the egg stage for *P. crinita* and *P. minor* (Ellertson and Ritcher, 1959).

Larval Biology

Hatching from eggs.—Larvae of the three species studied began hatching from eggs in late August and continued until late September. For comparative purposes, the earliest and latest dates of larval hatch are presented in Table 4 for all six Oregon species of *Pleocoma*. From the table, it appears that: (1) larvae of *P. crinita, P. minor,* and *P. oregonensis* begin hatching more than a month before the other three species; (2) *P. minor* and *P. oregonensis* larvae complete hatching earlier than the other four species; (3) the length of time between earliest and latest larval hatch is considerably less for *P. dubitabilis, P. simi,* and *P. carinata* than for the other three species.

Ritcher and Beer (1956) reported field-collected *P. dubitabilis* eggs produced larvae between 28 August and 8 September in 1954 and between 1 and 24 September in 1955.

Moulting.—In the soil, *Pleocoma* larvae prepare a cell in which to moult. The cell is usually cylindrical, rounded on the ends, and often horizontally oriented; if sloped at all, larvae usually lie with their heads at the upper end. Larvae almost always lie on their dorsa while moulting, often assuming this position a day or two before the moult and remaining on their dorsa for as long as 2 days afterwards.

First stage *Pleocoma* larvae moult about 1 month after hatching. Twenty-three first instar *P. carinata,* hatched in the laboratory from eggs deposited by two field-collected females, moulted for the first time between 5 and 12 October, approximately 33.5 days after hatching. Seventy first-instar *P. dubitabilis* (35 hatching from field-deposited eggs and 35 from laboratory-deposited eggs) moulted approximately 31 days after hatching. Larvae from field-collected eggs moulted between 21 September and 20 October, while those from laboratory-deposited eggs moulted between 30 September and 17 October.

Other than first instars, *P. dubitabilis* usually moult annually shortly before first instars leave the eggs. Of 55 *P. dubitabilis* larvae, field-collected between 24 July and 22 August 1961, the first moulted on 19 August and the last on 25 September. Eighty-four percent moulted between 26 August and 17 September.

Younger larvae seem to be the first to moult. Of 16 larvae that moulted prior to 1 September, 94 percent were fifth instars or younger and 69 percent were fourth instars or younger.

Some *Pleocoma* larvae, particularly first instars and those beyond their seventh year, may not moult each year. Out of 60 *P. dubitabilis* larvae collected between 24 July and 22 August 1961, 14 (23 percent) did not moult between the time they were collected and the time observations were discontinued in the laboratory on 15 October. All but one of these nonmoulting larvae were seventh instars or older, and all were males. First instar *P. dubitabilis* and *P. carinata* were observed daily from eclosion until 30 October and 6 November, 10 and 25 days, respectively, after the last larva of each species moulted. Of 80 first instar *P. dubitabilis* reared in the laboratory, five, or 6.3 percent, failed to moult. Twenty-one of 46, or 45.6 percent, first instar *P. carinata* failed to moult.

Sex ratio.—All larvae were sexed according to techniques described for some Scarabaeid larvae by Menees (1957) and Hurpin (1953). The applicability of their methods with *Pleocoma* larvae was confirmed when sexed larvae pupated, in which stage sex was readily determined (Ellertson and Ritcher, 1959).

Table 5. Sex ratio of three species of field-collected *Pleocoma* larvae.

Species	Number of larvae examined	Number of males	Number of females	Sex ratio males : females
Pleocoma dubitabilis	446	253	193	1.31:1.00
Pleocoma simi	114	64	50	1.28:1.00
Pleocoma carinata	77	43	34	1.26:1.00

Of all larvae collected in the field, males of all three species, *P. dubitabilis, P. simi,* and *P. carinata,* outnumbered females by 31, 28, and 26 percent, respectively (Table 5).

Six groups of first stage larvae, each group representing portions of larger egg clutches of six different females, were sexed to compute the larval sex ratio for progeny of individual females. Male to female sex ratios for first instars of *P. dubitabilis* and *P. carinata* range from a high of 2:22 to 1:00 to a low of 1:09 to 1:00 (Table 6).

Number of instars.—Head capsules of all larvae were measured at the widest portion of the dorsum to the nearest 0.15 mm. All head capsules of preserved specimens were dry when measured; no measurements were made with specimens submerged in preserving medium. Living larvae were anesthetized with a small amount of carbon dioxide while being measured.

The range of head capsule width for first and second instar *P. dubitabilis, P. simi,* and *P. carinata* was established in a manner similar to that used by Ellertson and Ritcher (1959). That is, several larvae were preserved shortly after hatching and measured to establish a range for the first instar. Other larvae were allowed to moult after which they were preserved and the head capsules measured.

Table 6. Larval sex ratio for progeny of individual females of *Pleocoma dubitabilis* and *P. carinata*.

Species	Number of larvae examined	Number of males	Number of females	Sex ratio males : females	Oviposition in:
Pleocoma	25	15	10	1.50:1.00	forest soil
dubitabilis	41	22	19	1.16:1.00	forest soil
	23	12	11	1.09:1.00	laboratory
	29	20	9	2.22:1.00	laboratory
Pleocoma	22	12	10	1.20:1.00	laboratory
carinata	22	14	8	1.75:1.00	laboratory

The range in measurements of head capsule width for first and second stage larvae of three species is shown in the following tabulation:

Species	Range in measurements (mm)		No. of larvae
	First instar	Second instar	
P. dubitabilis	1.95–2.55	2.25–2.55	118 and 92
P. carinata	2.25–2.55	2.55–2.85	44 and 23
P. simi	2.25 —	2.60 —	7 and 13

The range of measurements for *P. dubitabilis* and, to a lesser extent, *P. carinata* so overlap that there is no distinct difference in size of head capsules between the first two instars. The same is probably true for *P. simi.*

Frequency histograms for larval head capsule widths for all instars of all three species are shown in Fig. 3. The peaks for first and second instar *P. dubitabilis* and *P. carinata* are rather obvious; however, other than those peaks, an interpretation from the histogram of the range of any given instar for any of the species, especially *P. carinata* and *P. simi,* would be very subjective. Peaks may characterize some instars, at least with *P. dubitabilis,* but extremes of the range for each instar tend to merge.

With *P. dubitabilis,* it was possible by rearing larvae through a moult, to get two head capsule measurements on individual larvae, one prior to and one after the moult. Following this procedure and using the known range of second instars as a starting point, head capsule measurements have been arranged into reasonably discrete groups for the first eight instars (Table 7). From the data in Table 7 and the frequency histogram (Fig. 3A), minimum and maximum head capsule widths for the first eight instars are suggested as follows:

Tentative instars	Head capsule width (mm)	
	Minimum	Maximum
1	1.95	2.55
2	2.25	2.70
3	2.85	3.45
4	3.60	4.50
5	4.35	5.40
6	5.25	6.00
7	6.00	6.75
8	6.75	7.50

Although the ranges are given here for eight instars, it is obvious from Fig. 3A that *P. dubitabilis* larvae pass through more than eight stages. Moreover, the wide range of head capsule measurements for *P. carinata* and *P. simi*

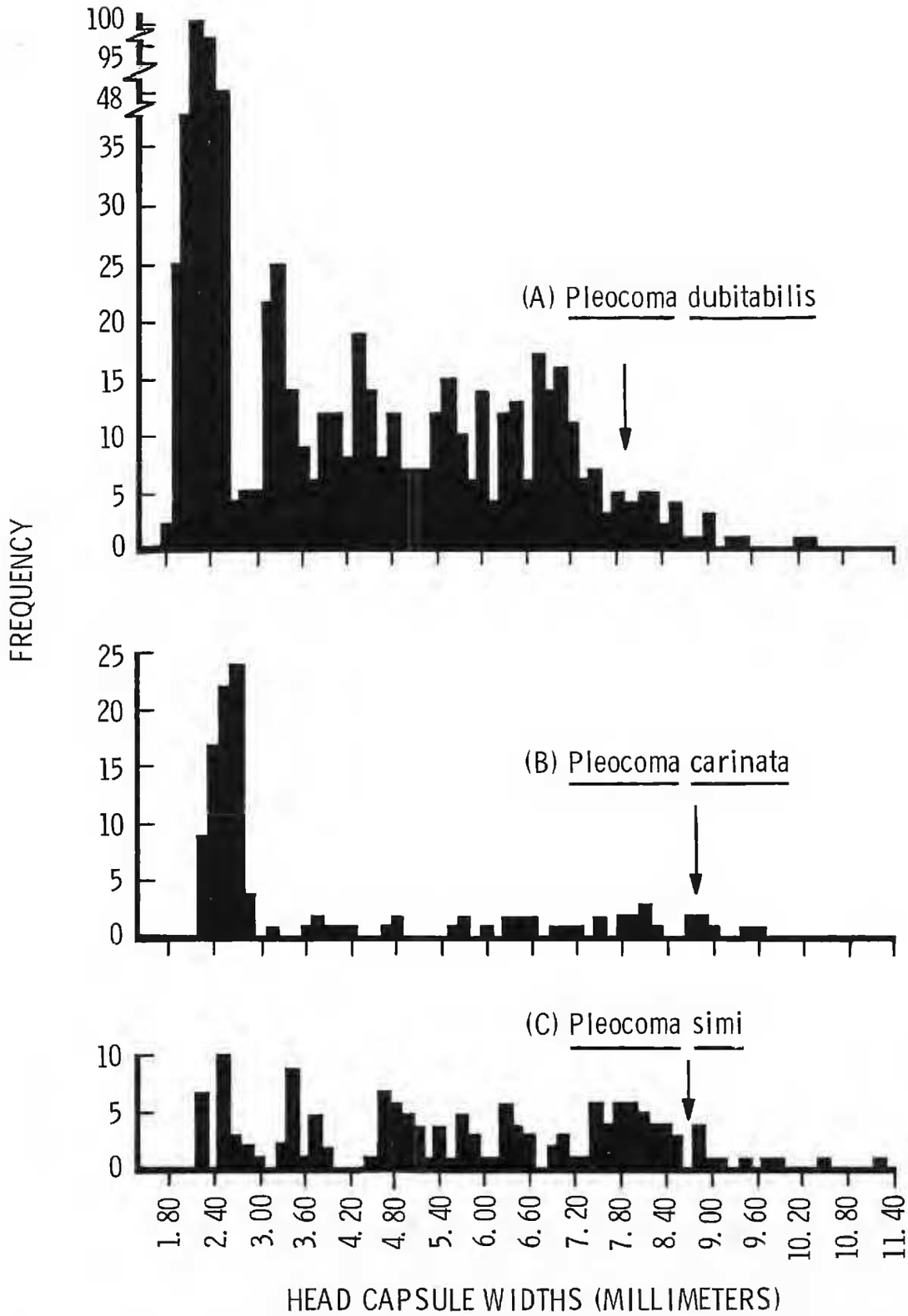

Fig. 3. Frequency histograms of larval head capsule widths for three species of *Pleocoma*. Portions of histograms to left of arrows represent both male and female larvae, portions to right represent females only.

(Fig. 3B, C) indicate that both of these species pass through as many instars as does *P. dubitabilis*.

There appear to be some sexual differences in the number of instars of *P. dubitabilis, P. carinata,* and *P. simi*. All larvae were sexed at the time

head capsules were measured and there appeared to be no difference in head capsule widths between sexes through about the eighth instar; however, with *P. dubitabilis,* all larvae with head capsules measuring more than 7.80 mm were females (Fig. 3A). The same phenomenon was observed with *P. carinata* and *P. simi* larvae; larvae of these two species with head capsules larger than about 8.70 mm were all females (Fig. 3B, C). Ellertson and Ritcher (1959) found that the largest *P. crinita* and *P. minor* larvae were all females. They found that three *P. crinita* larvae larger than 7.65 mm (9th or 10th instars) were females and the three largest *P. minor* larvae collected, all with head capsules greater than 7.95 mm, were all females.

Since there appears to be no difference in larval head capsule widths between sexes in the earlier instars, these observations indicate that in at least five species of Oregon *Pleocoma,* female larvae develop through more stages than males before pupating.

Pupation.—Pleocoma dubitabilis larvae appear to pass through at least seven instars before pupating. Six larvae that pupated had head capsules ranging from 6.45 to 8.25 mm as follows:

Sex	Head capsule width (mm)	Instar
Male	6.45	7th
Male	6.75	7th
Male	7.05	8th
Female	7.95	9th–older
Female	8.10	9th–older
Female	8.25	9th–older

P. dubitabilis larvae pupate toward the end of July, becoming inactive several weeks prior to the transformation. In 1961, larvae pupated between 20 and 31 July. Two larvae became completely inactive 41 and 72 days, respectively, before pupating. There are indications that some larvae become inactive as much as 6 months prior to pupating. At the McDonald Forest study area, most *P. dubitabilis* larvae pupated at relatively shallow depths in the soil, as shown in the tabulation:

Date of collection	Depth of pupae (cm)
27 July 1960	13.5
27 July 1960	13.5
25 August 1960	36.0
25 August 1960	50.0
28 January 1961	32.0
28 June 1961	40.0
13 September 1961	15.0

Table 7. Head capsule measurements of *Pleocoma dubitabilis* larvae made before and after moulting.

Head capsule width (mm) and tentative instar			Head capsule width (mm) and tentative instar		
Before moult	After moult	Increase (mm)	Before moult	After moult	Increase (mm)
2nd instars	3rd instars		5th instars	6th instars	
2.40	2.85	0.45	4.35	5.55	1.20
			4.35	5.70	1.35
3rd instars	4th instars		4.35	6.00	1.65
3.00	3.75	0.75	4.50	5.40	0.90
3.00	3.75	0.75	4.50	5.55	1.05
3.15	3.60	0.45	4.50	5.70	1.20
3.15	3.90	0.75	4.50	5.70	1.20
3.15	3.90	0.75	4.65	5.85	1.20
3.15	4.05	0.90	4.95	6.00	1.05
3.15	4.05	0.90			
3.15	4.05	0.90	6th instars	7th instars	
3.15	4.20	1.05	5.55	6.00	0.45
3.15	4.20	1.05	5.55	6.60	1.05
3.30	4.35	1.05	5.70	6.75	1.05
3.30	4.50	1.20			
			7th instars	8th instars	
4th instars	5th instars		6.00	7.50	1.50
3.60	4.65	1.05	6.30	6.90	0.60
3.75	4.50	0.75	6.30	6.90	0.60
3.75	4.80	1.05	6.30	6.90	0.60
3.75	4.95	1.20	6.30	7.05	0.75
3.90	4.65	0.75	6.45	7.05	0.60
3.90	4.80	0.90			
3.90	4.95	1.05			
3.90	4.95	1.05			
3.90	5.10	1.20			
4.05	4.80	0.75			
4.05	4.80	0.75			
4.05	5.40	1.35			
4.20	5.25	1.05			

At McDonald Forest, on 22 July 1954, Ritcher and Beer (1956) found three *P. dubitabilis* pupae at depths of 17.5, 18.5, and 24 cm. Generally, the depth of pupation is shallower in the soil than depths at which most larvae are found.

Natural control factors.—At the time of this study, no parasites or invertebrate predators had been reported from any species of *Pleocoma*.[4] Observations made during the study indicate that a fungus disease and a larval predator account for some larval mortality.

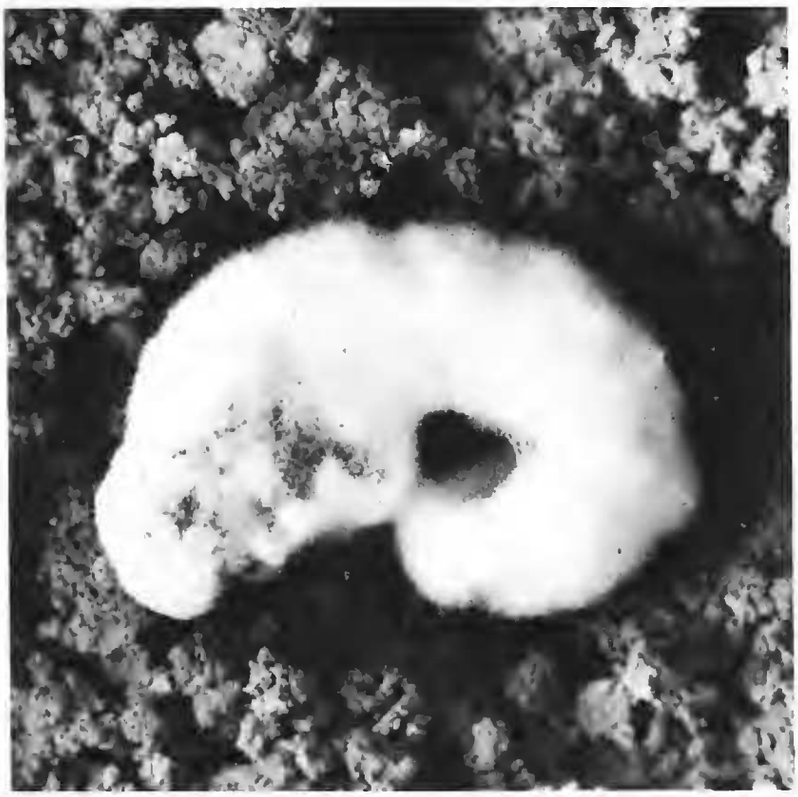

Fig. 4. Second stage *Pleocoma dubitabilis* larva killed by a fungus disease, *Beauveria* sp. (3×).

Five to 22 percent of the *P. dubitabilis* larvae collected in 1961 at the McDonald Forest study site had been killed by a fungus identified[5] as either *Beauveria globulifera* (Spegazzini) Picard or *B. bassiana* (Balsamo) Vuillemin. Infected larvae were collected in their soil burrows throughout the year and at depths ranging from 15 to 95 cm. All instars appeared to be susceptible. It is of interest that no diseased *P. simi* or *P. carinata* larvae were collected.

Observations made during laboratory rearings indicate that the fungus may develop quite rapidly in *Pleocoma* larvae even in relatively cool forest soil. In the laboratory, it took from 3 to 7 days at 9–11°C, for the *Beauveria* infection to progress from a state of apparent noninfection to a condition such as that shown by the larva in Fig. 4. Davis (1934b) reports having collected a number of *P. behrensii* pupae that had been attacked and killed by fungi.

Asilid larvae also kill some *Pleocoma* larvae. Occasionally, *P. dubitabilis* larvae were collected bearing discolored or blackened areas on one or more portions of the abdomen. On two occasions, dead or dying *Pleocoma* larvae were found with an asilid[6] larva in the burrow immediately adjacent to the grub; one grub had a hole in its thorax where the predator had been feeding. In both instances, the *Pleocoma* larva appeared similar to that shown in Fig. 5. Though only two *Pleocoma* larvae were collected that had been killed by asilids, these predators were frequently collected from sample

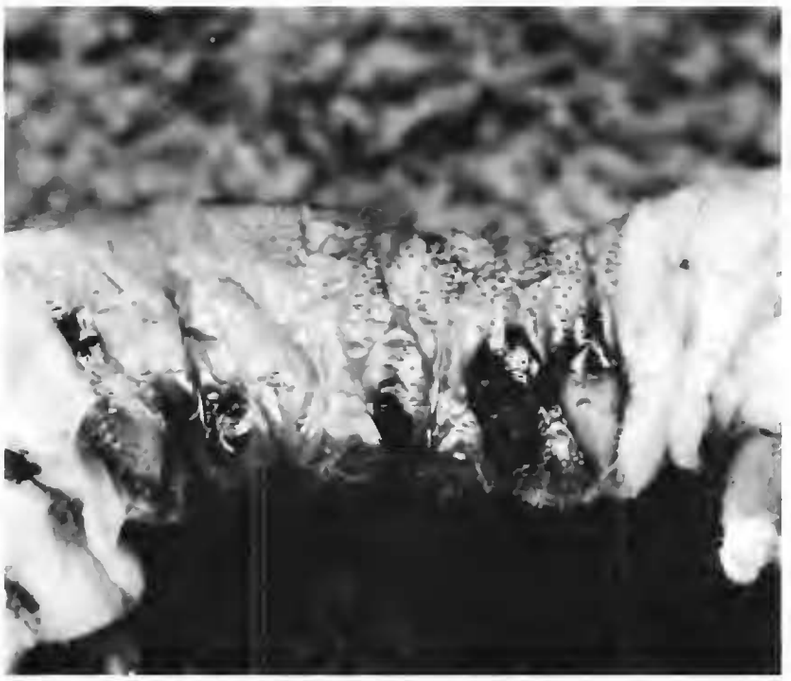

Fig. 5. A seventh instar *Pleocoma dubitabilis* showing discoloration in the abdominal mid-section and several blackened areas caused by feeding of a predaceous asilid larva (5×).

holes in the soil in the same general strata where *Pleocoma* larvae were found.

Hovore (1971) reports that *P. linsleyi* is ". . . preyed upon in the larval and pupal stages by a large dipteran larva . . . ." He and his colleagues have tentatively identified the predator as belonging to the family Asilidae, possibly in the genus *Stenopogon* (subfamily Dasypogoninae). He reports (1971) that he has collected these dipteran larvae from grubs and pupae of both sexes of *P. linsleyi* and has taken similar dipteran larvae from the immature stages of *P. badia,* and *P. venturae.* Hovore (personal communication) also reports having taken this asilid "parasitising" *P. fimbriata, P. marquai,* and *P. bicolor.* Asilids are known to be a natural enemy of other white grubs in the genus *Phyllophaga* (Davis, 1919) and, in one case, are reported to have controlled an infestation of *Phyllophaga koehleriana* (Saylor) in the Texas Panhandle (Daniels, 1966).

During this study, both ants and centipedes killed *Pleocoma* larvae that had been placed in the soil for experimentation; however, whether they kill larvae in the soil under natural conditions is not known. Ants do feed on other species of white grubs in the southeast (Anonymous, 1957).

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Footnotes

[1] This investigation was supported chiefly by the Oregon Agricultural Experiment Station and National Science Foundation Grants Nos. G-14296 and G-17935, and partially by the USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.

[2] According to Hovore (personal communication), the variety *dubitabilis* Davis was described in 1934 as a new variety of *Pleocoma staff* Schaufuss. Later, it was considered by Linsley (1938) to be a distinct species but inadvertently misspelled as *P. dubitalis*. This error has persisted since that time.

[3] The three observations on 12 November 1960 were made after larvae had hatched; however, the larvae had not dispersed from the niches in which the eggs had been laid.

[4] Collembola and mites have been reported to be associated with dead and living *Pleocoma* larvae in the vicinity of Hood River, Oregon, but whether either have acted antagonistically toward the grubs is not known (Ellertson, 1958).

[5] Identified by Clarence A. Thompson, insect pathologist, Forestry Sciences Laboratory, USDA Forest Service, Corvallis, Oregon.

[6] Identification of this asilid larva was confirmed by P. O. Ritcher, former Head, Department of Entomology, Oregon State University, Corvallis, Oregon.